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Collembola in Central Amazon inundation forests – strategies for surviving floods

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Summary. The soil of Central Amazonian inundation forests is subject to periodic flooding, which can reach a height of 4–5 metres and last up to seven months. Even after inundation, Collembola appear in high densities in the drying forest floor. Two strategies for recolonization were proven: mass-migration and survival through the production of flood-tolerant eggs. The ability to migrate is considered to be a general adaptation to the conditions in habitats in tropical forests. Flood-tolerant eggs could be an adaptation to the conditions of the inundation forests.

Key words: Collembola; Neotropics; inundation forests; mass migration; flood tolerant eggs

Introduction

Collembola are at an extreme disadvantage during unfavourable environmental conditions such as flooding during rainfall or after snow melt. Short term disturbances can be tolerated through dormancy in air bubbles for up to two months (Dunger 1983). However, long term inundation kills all animals except those surviving as specially adapted life stages. Central Amazonian inundation forests are subject to annual flooding for up to more than half a year with water level oscillations, in the largest rivers, of 10–15 metres. The fauna of the inundation forests, and their adjacent shore regions, comprise terricolous and arboricolous animals. Both include non-migrants and migrants. The migrating reaction of terricolous animals is horizontal (following the high-water line), vertical (temporal ascent to trunk or canopy) or includes a temporal flight to upland forests. Non-migrants have active or dormant stages under water (Adis 1992). Even after an inundation, Collembola reattain high densities in the drying forest floor. It is thus apparent that they possess strategies for recolonization of the forest floor immediately after flooding.

Materials and Methods

Experimental Sites

The investigations took place in a blackwater inundation forest, called "igapó" in Portuguese, bordering the Rio Negro near Manaus, Brazil. The igapós are inundated each year by extremely nutrient poor water from March to November. Two types of inundation forest, the "higher" and the "lower" igapó, are

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distinguished based on the distance from the river bed and the duration of flooding (Adis 1984). In the area of the investigation, the water advances into the forest up to approximately 250 m. In the high-water situation, during July, the water level in the lower igapó reaches 5 metres above ground. Here the inundation can last for up to seven months. The forest floor is covered by a thin litter layer of 2–3 cm in thickness.

Pitfall traps

Pitfall traps, with directed openings, were used to study migration (Fig. 1). The openings had a width of 10 cm. To avoid disturbance, caused by digging the traps in, tubes were dug into the soil before flooding and the traps themselves were set in the tubes for 24 hours when water levels were falling on the 11th to 12th of September, 1990. On 11th September, the traps were located 10, 70, 100, 130, 160, and 190 m away from the receding floodwaters. At each distance four traps were installed, two with openings towards the water, thus capturing animals migrating away from the floodwaters, and two traps with openings pointed in the opposite direction, capturing animals migrating towards the water. During the last 48 hours before removing the traps, the water edge receded by about 40 metres. Picric acid was used to kill the animals.

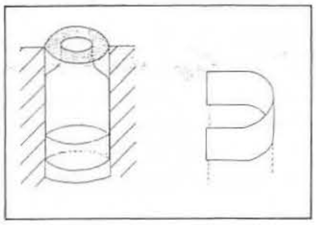

Fig. 1. Pitfall trap with shield

Flood boxes

To investigate the hatching of Collembola from inundation resistant eggs, litter was exposed to flooding in litter-boxes. The boxes were constructed of frames of wire, measuring 36 × 30 × 8 cm, and covered with gaze of 1 mm mesh. They were set out on the forest floor two weeks before the inundation of the lower igapó and removed following 179 days of inundation, a few days before dryfall. The litter was incubated for 14 days in buckets and the Collembola subsequently extracted by heat over a period of 14 days in a Kempson apparatus (Adis 1987).

Soil samples

To study the abundance and phenology of Collembola after dryfall of the forest floor, eight soil samples were taken at the water's edge in the lower igapó on 11. 9. 1990 and two weeks later (25. 9. 1990) at the same site on. The soil samples had diameters of 21 cm and were taken to a depth of 7 cm. For extraction in the Kempson apparatus they were split into 2 discs each 3.5 cm in depth.

Results

The results of the pitfall traps showed mass migration of Collembola, following the receding water (Fig. 2). Within 10m. of the water's edge, *Brachystomella* were most abundant, with more than 1000 individuals (sum of two traps). However, *Proisotoma* and *Dicranocentrus* were also abundant. At 70m., *Dicranocentrus* followed in its own migration wave, and at a distance of 100 m. a peak of *Lepidocyrtus* was observed. At greater distances from the floodwater edge, the migration waves pass into local undirected wanderings with low numbers of individuals. The other genera showed no directed migrations or migrated in low numbers. Symphypleona showed only local undirected wanderings.

The genera occurring in high numbers in the flood boxes were found only irregularly in pitfall traps (Fig. 3). These were the genus *Isotomiella*, the Symphypleones *Collophora* and *Cal-*

vatomina, and the Poduromorpha, *Onychiurus* and *Mesaphorura*. Only *Proisotoma* appeared in both the flood boxes and were highly abundant in the pitfall traps. The eggs of only two genera of Entomobryomorpha, *Isotomiella* and *Proisotoma* (both Isotomidae) were able to withstand the flood for 179 days.

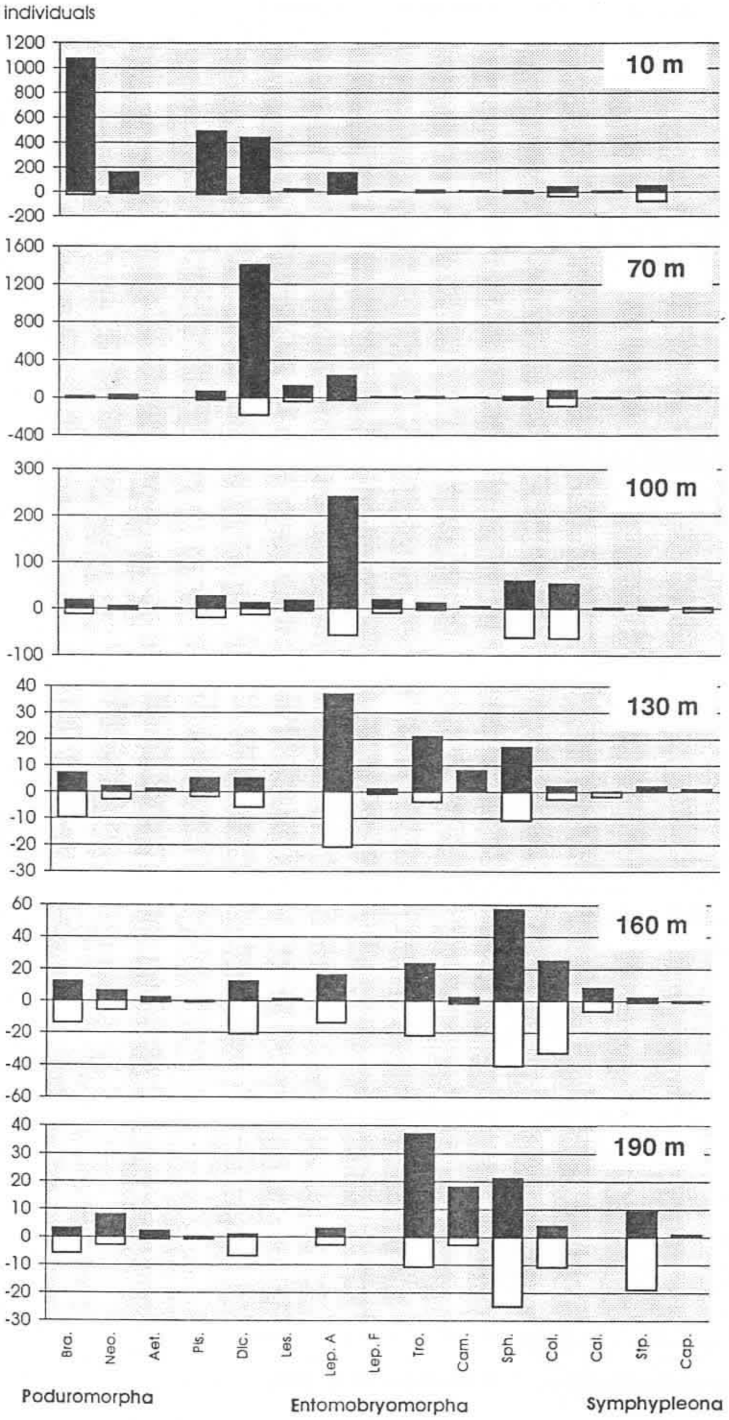

Fig. 2. Numbers of individuals of some genera collected in pitfall traps opening in one direction only. Positive numbers: animals migrating towards the floodwater, negative numbers: migrating in the opposite direction. Distances in metres to the water's edge. Abbreviations of generic names in this and following figures: Bra.: *Brachystomella*, Cal.: *Calvatomina*, Cap.: *Caprainea*, Col.: *Collophora*, Dic.: *Dicranocentrus*, Hyl.: *Hylaeanura*, Iso.: *Isotomiella*, Lep. A: *Lepidocyrtus A*, Les.: *Lepidosira*, Meg.: *Megalothorax*, Mes.: *Mesaphorura*, Neo.: *Neotropiella*, Ony.: *Onychiurus*, Par.: *Pararrhopalites*, Pis.: *Proisotoma*, Sph.: *Sphaeridia*, Spy.: *Sphyrotheca*, Stp.: *Stenognathriopes*, Tro.: *Trogolaphysa*

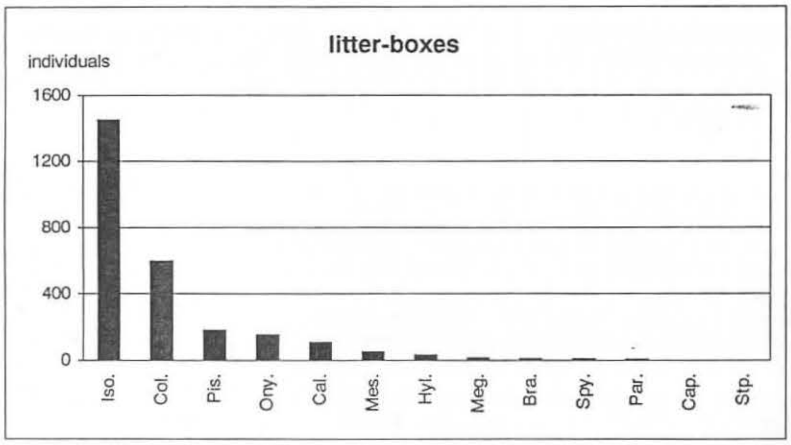

Fig. 3. Numbers of individuals in flood-boxes. Means are calculated for 500 g dry litter from 4 boxes

The abundances of Collembola in the soil samples on 11. 9. 1990 (Fig. 4) showed the same pattern as the pitfall traps nearest the water. The most abundant genera were *Proisotoma* and *Brachystomella*, with nearly 17,000 and 8,000 individuals m^{-2} respectively. Two weeks later, on 25. 9. 1990 (Fig. 5), the situation had changed drastically with *Isotomiella* being dominant (13,000 m^{-2}) and representing more than 50% of the individuals extracted. Other genera which were also present in the flood boxes, such as *Onychiurus*, *Mesaphorura*, and *Collophora*, first appeared in the soil on the second sampling date. On that date, *Proisotoma* and *Brachystomella* showed much lower mean abundances of about 600 individuals m^{-2}.

Discussion

Mass migrations of Collembola are observed frequently during winter months in the northern hemisphere. They occur as colonies in patches or lines with distinct limitations, moving in one direction. This behaviour may be connected with reproduction or the search for food (Lyford 1975; Hågvar 1995). In the floodplain forests, migration can be considered as a strategy for recolonization of the forest floor as it dries. Although vertical migration on trees

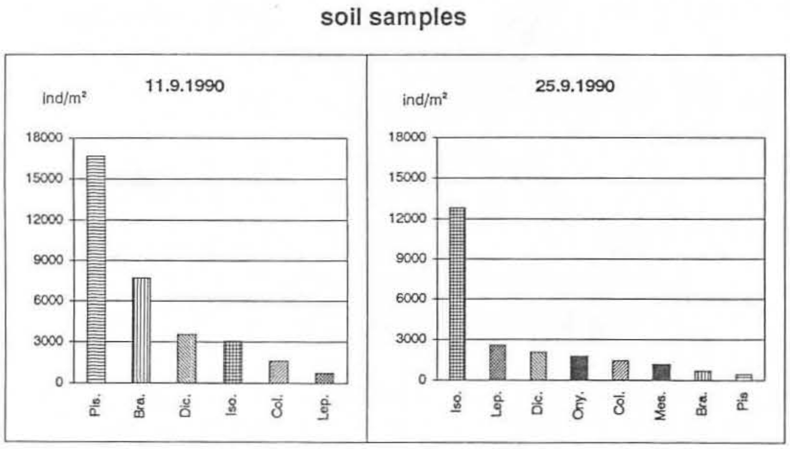

Fig. 4/5. Abundances in soil samples collected on 11. 9. 1990 and 25. 9. 1990 has been shown to be used by other animals (Adis 1992) it appears to play a minor part for Collembola. Collembola do climb up trees in high numbers (up to 3400 individuals in 14 days per tree, Adis, unpublished dates) during floodwater rises but relatively few animals (ca. 100 individuals per week and tree) could be collected when water levels fell. Most of these animals belong to genera, which were not collected on the forest floor (*Xenylla, Seira, Cyphoderus*).

The migrating Collembola do not appear as moving colonies but as a directed "migration-field". For example, *Brachystomella* appeared in the trap nearest the water's edge at a mean rate of 21 individuals per hour in a line of 10 cm in length. Similarly, *Proisotoma* showed a dense wave of migration following the waterline. This observation corresponds with the high abundance of these genera in the soil samples near the water's edge. These results suggest, that *Proisotoma* and *Brachystomella* can migrate quickly, following optimal environmental and nutritional conditions.

High vagility can be considered as an adaptation to spatially and temporally non-foreseeable changes in the habitats of tropical forests. For Collembola inhabiting the inundation forests, the ability to migrate can serve as a preadaptation for quick use of optimal conditions in the habitat after flooding. These consist of high humidity in the soil and a supply of organic particles and algae from the sediments of the retreating floodwaters (Walker 1992). These conditions only occur for short periods in the drying soil. After a few days, these Collembola are at a disadvantage due to the increasing dryness and scarcity of food and disappear from the forest floor, as was shown in the soil samples two weeks later. *Dicranocentrus* and *Lepidocyrtus* migrate much more slowly, following the retreating water edge at greater distances. These two genera were present in higher abundances in the soil samples only after two weeks.

The Symphypleone, *Collophora* and *Calvatomina*, and the Isotomid, *Isotomiella* did not appear in the pitfall traps; however, they were abundant in the flood boxes and in both soil samples. It is thus apparent that these Collembola do not migrate but hatch from eggs laid before flooding begins. After inundation they develop quickly, i.e. during the 14 days of extraction from the soil samples in the Kempson. The Poduromorpha, *Mesaphorura* and *Onychiurus*, also appeared in the flood boxes, but only in the second soil sample. They thus develop from eggs more slowly than the Symphypleones and *Isotomiella*.

Flood resistant eggs, subject to inundation for up to seven months in oxygen-free water, can be considered to be a direct adaptation to the conditions in the inundation forests.

From the results of these studies, the following strategies for recolonization of the forest floor can be distinguished: (i) fast horizontal migrations where animals appear, in high abundances, directly behind the retreating water edge; (ii) slow horizontal migration where animals follow the retreating water at greater distances; (iii) fast development from eggs laid before flooding with animals appearing with high abundances and adult individuals some days after the flood and (iv) slow development from eggs laid before flooding with adult individuals of these animals only appearing some weeks after the flood.

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